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Subfossil statoblasts of *Lophopodella capensis* (Sollas, 1908) (Bryozoa, Phylactolaemata, Lophopodidae) in the Upper Pleistocene and Holocene sediments of a montane wetland, Eastern Mau Forest, Kenya

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Abstract

Lophopodella capensis (Sollas, 1908) is only known from a limited number of palustrine and lacustrine sites in southern Africa and single sites in both Kenya and Israel. Statoblasts of *L. capensis* were found preserved in the Upper Pleistocene and Holocene aged sediments of Enapuiyapui wetland, Eastern Mau Forest, western Kenya. The wetland is a headwater microcatchment of tributaries that feed into the Mara River and the Lake Victoria Basin. Bryozoan taxa were not surveyed in a 2007 macroinvertebrate biodiversity assessment. The presence of *L. capensis* at this site marks the second observation of this taxon in Kenya, 65 km from Lake Naivasha, where observed prior, and in a location some 1000 meters higher. The results suggest Bryozoa should be included in aquatic biodiversity surveys that target these wetlands and that bryozoan remains should be incorporated into palaeoecological studies as useful palaeoenvironmental indicators.

Keywords

Aquatic, biogeography, distribution, freshwater, fossil, statoblasts, subfossil, Mara River, palaeodistribution, palustrine, range

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Introduction

Lophopodella capensis (Sollas, 1908) (Bryozoa: Phylactolaemata: Lophopodidae) is a small Bryozoan that is epiphytic on stems and leaves and epilithic and occurs in fresh-water to brackish waters, up to 9.4 pH in a temperature range of 18–25 °C (Lacourt 1968). It has been observed at water depths from littoral to 18 m depth (Lacourt 1967). *L. capensis* specimens were originally described from Vlei, Cape town, South Africa, in 1908 (collected in October 1907), and has since then been documented at other locations including Namibia in 1911 (Kraepelin 1914), multiple sites in the Transvaal since 1928 (Hastings 1929), Lake Naivasha, Kenya (Jenkin 1936), and more recently in the Golan Heights, Israel in 1967 (Massard and Geimer 1991). Additional reports of specimens from sites in Japan and UK, but, these have not been confirmed with certainty. The chitinous asexual buds (statoblasts) of Phylactolaemata preserve well within the geologic record of the Upper Quaternary and have potential for interpreting palaeoenvironmental conditions and examining the natural history of identifiable taxa (Francis 2001). Here we present a second occurrence of *L. capensis* in Kenya from subfossil statoblasts observed in the Upper Pleistocene and Holocene aged sediments of a small, montane wetland located in the Eastern Mau Forest.

Study region

Kiptunga Forest Block is located in the Eastern Mau Forest Block, Mau Narok County, Kenya, and is managed by a local Kenya Forest Service (KFS) station (Figure 1). The Eastern Mau Forest is the smallest of the Mau Forest blocks and has been identified as the most susceptible to negative impacts caused by anthropogenic land use, land cover, and global climatic changes, yet, has high potential for ecological restoration and recovery (Kinyanjui 2011). The region is situated upon the Mau Escarpment that forms part of the western face of the Great Rift Valley. The geology consists of undifferentiated Tertiary volcanic rocks overlain by Tertiary eutaxitic welded tuffs, which are evident in streambeds and occasional outcrops. The surficial geology consists of an extensive, thick mantle of Upper Pleistocene Mau ashes with basal tuffs (Jennings 1971, Williams 1991), possibly sourced from Londiani and/or Kilombe. Soils consist of relatively young and productive Udands (Andisols) due to the humid orographic climate modifying the abundant volcanic tephra. The mantling and subsequent aeolian and hydrological reworking of the tephra deposit may have formed much of the topographic relief of the ridge including the shallow basin where the wetland subsequently developed.

The indigenous forest is diverse with abundant Afromontane taxa including *Croton*, *Dombeya*, *Ficus*, *Juniperus*, *Olea* spp., *Podocarpus*, *Polyscias*, *Prunus* and *Schefflera*, of which, remnant scattered minor pockets remain. Most of the indigenous forest has been cut and converted to agroforests by the 1930s (Troup 1932) and the forest vegetation is currently partitioned into plantations with cyclic harvesting (Okeyo-Owuor 2007, Sanya 2008). Plantation taxa include indigenous *Juniperus procera* and, increasingly, exotic

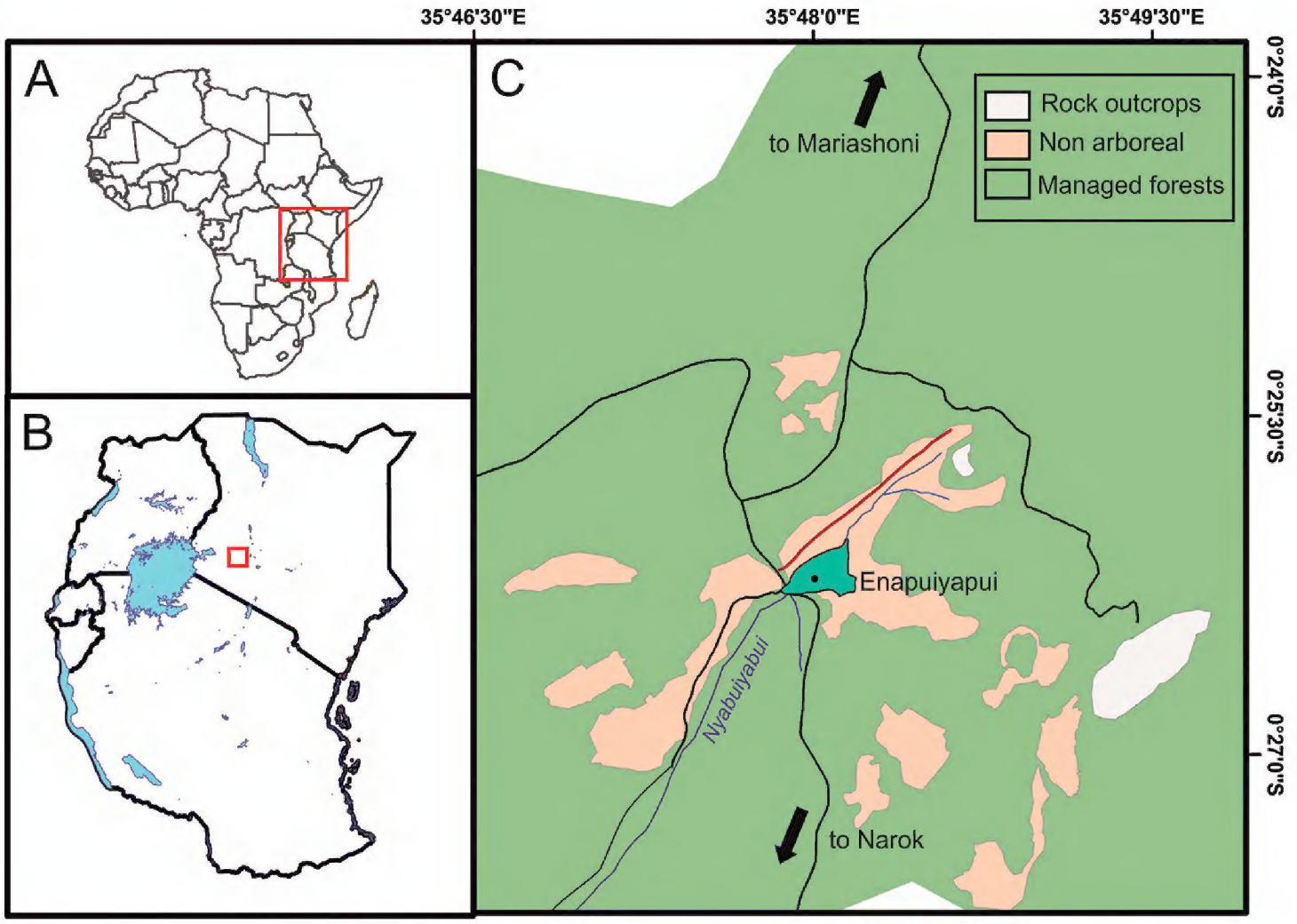


Figure 1. Location of the study site in Africa (**A**) and within Kenya (**B**). The location of the coring site (black circle) within Enapuiyapui (**C**). The red line represents a fire break cutline.

taxa are planted, which include *Pinus patula*, *Cupressus lusitanica*, *Corymbia maculata* (syn. *Eucalyptus maculate*; Sanya 2008, Courtney Mustaphi et al. 2014). Stresses on the plantation forests include pests, such as insects, rodents, monkeys that may damage the apical buds of *Pinus* and *Cupressus*, and fires during dry periods. Kiptunga Forest hosts wildlife populations of birds, antelopes, gazelles, hyrax, small reptiles, small primates and hyenas (Okeyo-Owuor 2007). A survey of macroinvertebrate taxa conducted in April 2007 found 606 families but did not observe any Phylactolaemata (Okeyo-Owuor 2007). The region is inhabited by the Ogiek community who are traditionally practiced hunter-gatherer livelihoods but current local populations are increasingly practicing pastoralism, dominantly cattle, goats and sheep, and much of the lower elevations have been converted to sedentary agriculture (Spruyt 2011).

Materials and methods

Sampling site

The site is 65 km and just over 1000 m above Lake Naivasha, the nearest documented observation of *L. capensis*. Enapuiyapui (0°26'11.28"S, 35°47'58.74"E; 2920 m asl,

Figures 1–2) is a high elevation wetland that is an important headwater of Nyabui-yabui, a stream that is an upper tributary of the Mara River, which flows through a landscape characterised byagroforestry patches, productive agricultural areas and the Maasai Mara National Reserve and Serengeti National Park before flowing into Lake Victoria. Enapuiyapui is hydrologically important, being one of the 'water towers' of orographic precipitation in Eastern Africa, which is undergoing rapid changes in water levels due to land use and land cover change and the interaction with regional climate change (Okeyo-Owuor 2007). The swamp is located along the broad ridge of the Kiptunga Forest Block and is highly sensitive to hydroclimatic changes and anthropogenic modifications; expanding and contracting in response to local hydroclimatic conditions. During periods of heavy rainfall there are minor ephemeral inflows and under wetland high stands a single outflow to the southwest; forming a tributary of the Amala and Mara Rivers. The wetland supports a floating vegetation mat during wetter periods. The greater wetland covers an area of 122 ha although the current 'wet swamp' area is about 6 ha. Logging access roads have been constructed to the north, west and south sides of the wetland and includes a bridge over the outlet. The swamp is shallow with most water depths well below 50 cm during March-April 2014 and was lower still (<20 cm) during April 2015. The water level has been decreasing and some locals anecdotally mentioned that there was open water within the swamp and a channel to the road bridge prior to 1972. Interview studies suggest that water levels are certainly lower than 30 years prior with minor degradation of water quality (Okeyo-Owuor 2007). There is some evidence of recent human modifications of the wetland including the bridge construction over an outlet channel, a cut line running along the west margin to keep grass fires from threatening the forests, an abandoned, pumping station built by the colonial government immediately to the east of the bridge that used to supply water to the Kiptunga Forest Station. Cattle graze along the dry margin and further impact the hummocky ground and morphology of the Poaceae and Juncaceae-dominated tussocks.

The swamp is continuously covered by Cyperaceae-Poaceae dominated vegetation with patches of Juncaceae (Figures 2–3). Some tussocks of Cyperaceae, Poaceae and/or Juncaceae provide microhabitat for small forbs and ferns. It is surrounded by Cyperaceae-Poaceae within the dry edges within the basin and there are small patches of indigenous forest and monoculture tree plots above the basin. Surrounding plantation stands are of variable ages with planting dates from 1935–2006 with the majority of stands dating from the 1960s (Sanya 2008, Courtney Mustaphi et al. 2014). Plantations of *Cupressus lusitanica* dominate the area surrounding the wetland.

Sample collection

On the 10–12 April, 2014, surface sediment samples were collected from 19 locations within the wet area of the swamp and the immediate surrounding region that has been ephemerally wet over the past century. To locate the thickest sediment accumulation

Figures 2–3. An wide angle aerial oblique photograph of Enapuiyapui wetland from the northwest facing southeast (**2**). Coring the center of the Cyperaceae-Poaceae wetland, April 2014 (**3**).

area of the swamp to target for coring the complete stratigraphy, the wetland was first probed using fiberglass rods with multiple 1-m-long rod extensions. A 537 cm stratigraphy was collected near the swamp center using a hand pushed Russian D-shaped corer in 50 cm drives with approximately 10 cm overlapped sections (Figure 3). Cores

were wrapped in plastic wrap and aluminum foil, shipped to the University of York, UK, and refrigerated at 4 °C. At the Department of Geography and Earth Sciences, Aberystwyth University, UK. The core sections from 484 cm deep to the top where optically imaged with a RGB camera and volume magnetic susceptibility was simultaneously measured with a Bartington MS2E sensor at continuous 1 cm intervals and air corrected between measurements.

Subsamples of 1 cm^3 were extracted at 1-cm intervals from 537 cm to the top and extracted from the wet core. Subsamples were put in a labelled beaker and soaked with a sodium hexametaphosphate solution ($Na_6P_6O_{18}$) and drop of hydrogen peroxide (H_2O_2) to disaggregate the samples and aid in the separation of the organic material and the clay particles (Bamber 1982). Samples were wet sieved through a 125 μm mesh and the retained organic and sediment material was visually inspected under a Zeiss Axio Zoom V16 microscope at 10–40× magnifications. Observations of macroscopic remains of taxa represent presence data only.

The chronology of the stratigraphy was developed through radiocarbon dating, development of an age-depth model to assign ages to the sediment core depths, and stratigraphic zonation of the magnetic susceptibility data showed periods of significant change in the sediments. Nine samples of organic sediments and organic detritus were accelerator mass spectrometry (AMS) radiocarbon dated and an age-depth model was produced and parameterization is described in the caption of Figure 4. Stratigraphic zones were delineated in the magnetic susceptibility data using a regime shift index sequential algorithm (RSI, Rodionov 2004). Magnetic susceptibility values reflect changes in the erosion patterns and deposition of the sediments of the catchment into the basin (Dearing 1999). The difference between weighted means of the magnetic susceptibility temporal regimes, with a minimum cut-off length of 50 cm, were tested for significance with a Student's two-tailed t-test with unequal variance (Huber's weight function parameter = 5) at $P < 0.01$.

Data resources

The data reported in this paper have been deposited to the Harvard Dataverse repository (Courtney Mustaphi et al. 2016) at http://dx.doi.org/10.7910/DVN/ONKLLL.

Results

Sediment stratigraphy

The basal date for the sediment stratigraphy was 16600 yr BP and represented the onset of organic sediment accumulation that has continued to present (Figure 4). Three radiocarbon dates were excluded from the age-depth model because they may have contained organic matter that was not representative of the stratigraphy (Figure 4, Table 1).

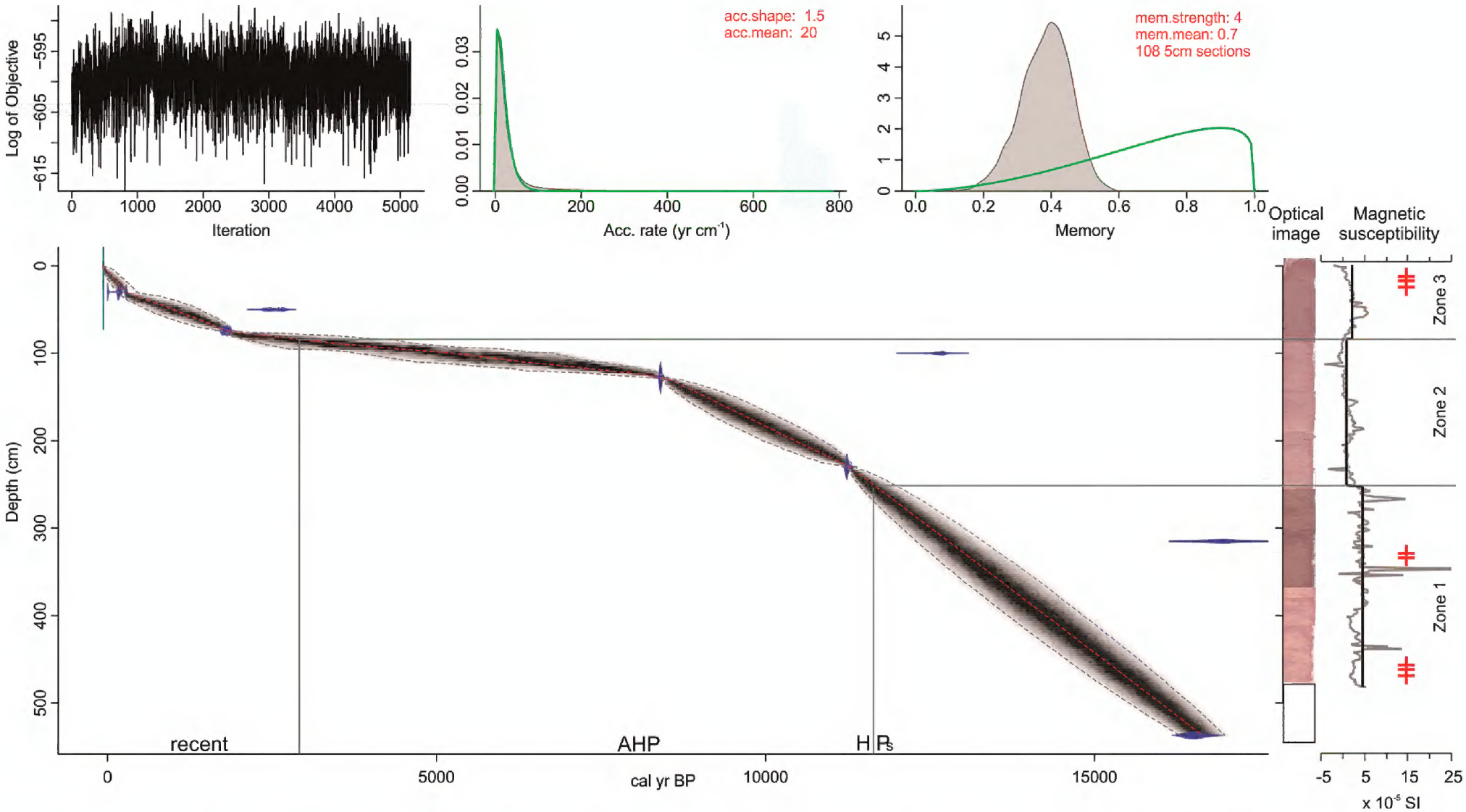


Figure 4. BACON version 2.2 R program language script age-depth model for the Enapuiyapui stratigraphy using MCMC random walks (greyscale shading) through the probable radiocarbon dates (1σ age probability distributions represented in blue) that were calibrated using the IntCal13 curve (Table 1; Blaauw and Christenson 2011; Reimer et al. 2013; R Development Core Team 2015). The final model used the weighted average of the random walk densities (red line) and 95% CI (dotted grey lines) and parameter settings are shown at the top right (red font). Ages reported as calibrated year BP (before present, 1950 CE). ITRAX optical core face photographs and magnetic susceptibility profile (grey line) at bottom left that shows the 484–0 cm section of the 537 cm core. Zones were defined using a regime shift index of the magnetic susceptibility values (Rodionov 2004). *Lophopodella capensis* presence data are represented by red '+' symbols on the magnetic susceptibility profile. Abbreviations are AHP: African Humid Period, H: Holocene, Ps: Pleistocene.

Table 1. Age determinations for the 537 cm Enapuiyapui Swamp stratigraphy. *1σ error. pMC, percent modern carbon, defined as 1950 common era by ^{14}C activity standard. ** Dates that were excluded from the age-depth modelling.

Depth (cm)	Age (^{14}C years)*	pMC*	$\delta^{13}C_{VPDB}$ (±0.1 ‰)	Material	Laboratory ID
0	–64			Top of core	
30–31	201 ± 23	97.53 ± 0.28	–27.3	Picked organics	D-AMS-009664
50–51	2449 ± 35	73.72 ± 0.32	–23.5	Bulk sieved <63μm	SUERC-57340**
74–76	1865 ± 37	17.58 ± 0.13		>63μm charcoal	UBA-27553
100–101	10721 ± 47	26.33 ± 0.15		Bulk sediment	UBA-26117**
128–129	7616 ± 33	38.75 ± 0.16	–24.5	Picked organics	D-AMS-009663
230–231	9837 ± 42	29.39 ± 0.15		Bulk sediment	UBA-26118
315–316	13963 ± 60	17.58 ± 0.13		Bulk sediment	UBA-27554**
537	13692 ± 83	18.19 ± 0.19		Bulk sediment	UBA-26116 (Base)

Alternative models were considered but did not impact the probable age ranges of the presence of the *L. capensis* subfossil remains. The sediments were uniform, massive deposits composed of highly organic sediments with silt and few sand-sized clastic material derived from the tuff deposits surrounding the basin. The magnetic susceptibility values ranged from –4 to 70 $\times 10^{-5}$ SI and averaged 2.8. The variability in the magnetic profile was divided into three zones (Fig. 4): 1) 537–254 cm (16600–11700 yr BP), 2) 253–85 cm (11700–3000 yr BP), 3) 84–0 cm (3000 yr BP to present). These zones broadly reflect regional hydroclimatic changes related to solar variation driven influences on the African Monsoon pattern (Shanahan et al. 2015).

Lophopodella capensis remains

The examination of 19 surface sediment samples collected in April 2014 did not yield any Phylactolaemata remains from any location within the wetland (Table 2). The chitinous remains of fully developed statoblasts of *Lophopodella capensis* were observed in 13 of the 537 samples (2.4%) of the sediment stratigraphy levels from the center of the wetland (Figure 4, Table 3). When individual intact statoblasts were present, the concentrations ranged between 1 and 6 statoblasts per cm^3 of wet sediment. These were found in three clusters in the stratigraphy: between 482–465 cm, representing 15700–15400 yr BP and again during the Upper Pleistocene at 345–331 cm 13300–13000 yr BP. The most recent presence was between 42–16 cm, during the recent upper Holocene sediments aged 710–120 yr BP. All of the elliptical statoblasts encountered had polar spines that were split between the two layers, a common circumstance in contemporary-aged specimens and described by Sollas (1908) and Lacourt (1968).

Table 2. Surface sediment sampling locations and volume of wet sediment analysed for *L. capensis* remains.

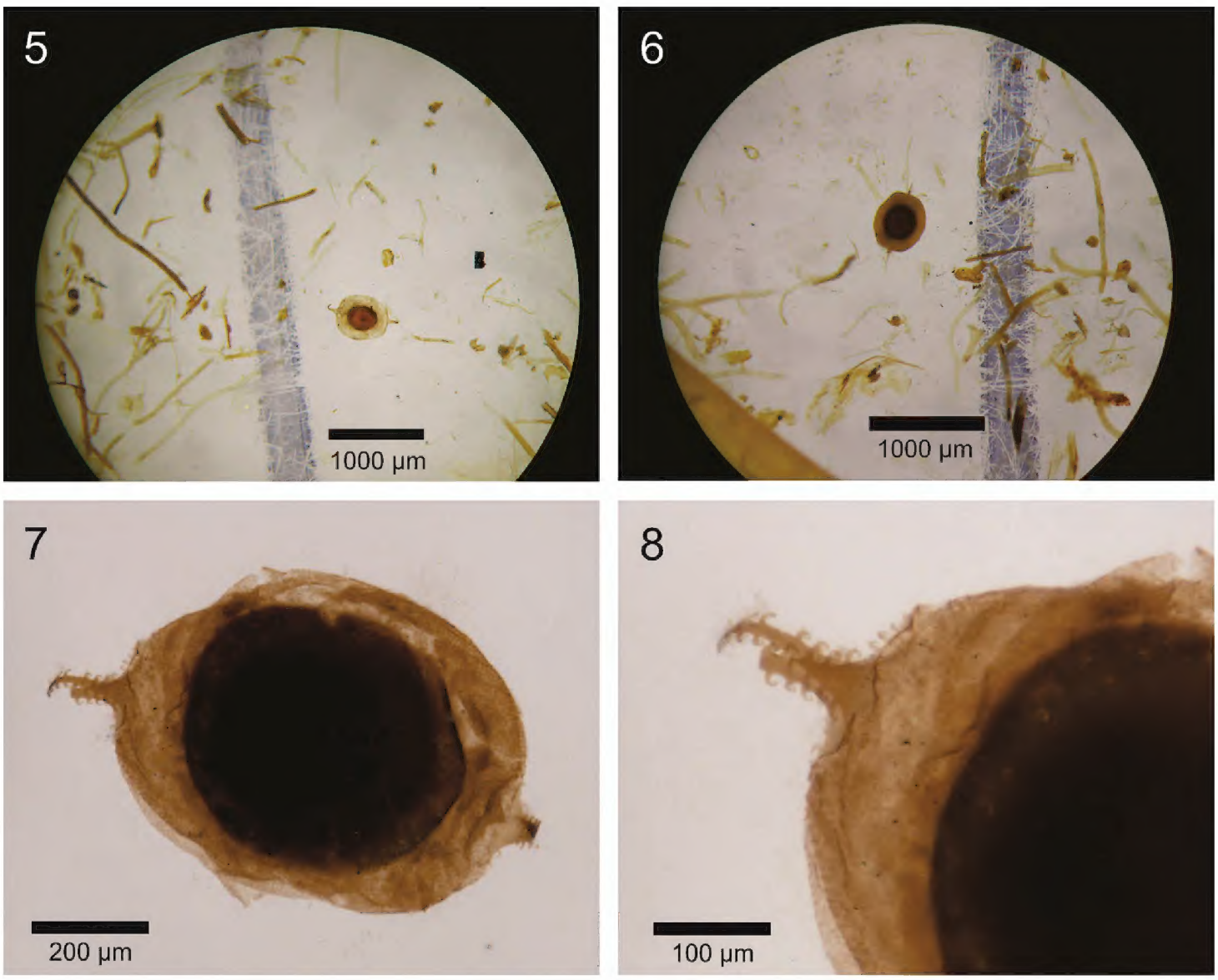
ID	Latitude	Longitude	Volume (cm^3)
NB 1	-0°26.226'	35°47.870'	1
NB 2	-0°26.196'	35°47.892'	1
NB 3	-0°26.242'	35°47.891'	1
NB 4	-0°26.232'	35°47.954'	1
NB 5	-0°26.235'	35°47.995'	1
NB 6	-0°26.231'	35°48.025'	1
NB 7	-0°26.224'	35°48.044'	1
NB 8	-0°26.221'	35°47.888'	1
NB 9	-0°26.190'	35°47.959'	1
NB 10	-0°26.197'	35°47.940'	1
NB 11	-0°26.218'	35°47.922'	1
NB 12	-0°26.199'	35°47.903'	1
NB 13	-0°26.178'	35°47.889'	1
NB 14	-0°26.175'	35°47.906'	1
NB 15	-0°26.176'	35°47.923'	1
NB 16	-0°26.177'	35°47.935'	1
NB 17	-0°26.163'	35°47.947'	1
NB 18	-0°26.133'	35°47.919'	1
NB 19	-0°26.121'	35°47.908'	1

Table 3. Depth intervals and modeled ages of presence of *L. capensis* remains presented as concentrations of statoblasts per volume of wet sediment.

Depth interval (cm)	Age interval (yr BP)	*L. capensis statoblasts* per cm^3
16–17	117.6–129.7	2
20–21	166.1–177.1	1
21–22	177.1–188.5	1
22–23	188.5–199.8	1
23–24	199.8–210.9	3
25–26	221.9–233.8	1
26–27	233.8–245.7	2
41–42	670–711.6	1
331–332	13058.4–13075.3	1
344–345	13285–13302.3	1
465–466	15392.7–15410.4	1
480–481	15655.3–15671.8	6
481–482	15671.8–15688.3	4

Discussion and conclusions

Neither *Lophopodella capensis* nor other Phylactolaemata taxa were encountered in a macroinvertebrate survey conducted across the swamp in April 2007 (Okeyo-Owuor 2007). Although, the survey does not explicitly state whether bryozoans were target taxa for surveying, nor are there details if they were observed or known to be absent. No macroscopic (>125 μm) bryozoan remains were observed in subsamples from the 19 surface sediment samples collected across the wetland. *L. capensis* were present in three clusters in the stratigraphy and suggest that *L. capensis* was present in the wetland since at least 15600 yr BP and was certainly present until recently, around 120 yr BP (Figure 4). Preservation was variable and suggests that degradation of chitinous material has varied throughout the ontogeny of the wetland (Figures 5–8). Presence data represent local presence of the taxa; yet, absence cannot be conclusively interpreted as absence of the taxa in the palaeoenvironment nor present. The historical presence of *L. capensis* at Enapuiyapui, a montane headwater wetland, suggests range and biogeography may be influenced by animal dispersal. Although not observed related to *L. capensis*, birds have been shown to be associated with the distributions of some freshwater bryozoans (Freeland et al. 2000; Figuerola et al. 2005). Possible pathways include feather and skin attachment and ingestion and subsequent excretion after traveling (Brochet et al. 2010). Since waterborne dispersal is possible by lophopodid taxa (Wood 2009), the ecological range may include parts of the Lake Victoria Basin and ultimately the Nile, at least during certain intervals of the Late Pleistocene and Holocene. Similar to other lophopodid, *L. capensis* may be adapted to seasonal drought or possibly extended, multi-year dry periods (Wood 2009). Unlike most other phylac species, the free statoblast of a related taxa, *L. carteri*, is initially non-buoyant and sinks through the water column, is deposited at the bottom of the basin, to be covered by sediments. During drought conditions, the water dries up and the statoblasts are protected from direct sunlight. As the statoblast dries the water in the large annulus is replaced by air, making the entire structure very buoyant once water returns. Once refloated to the water surface it can germinate within a few days. If a lake does not dry up the statoblast will still eventually germinate if the water-sediment interface temperature is sufficiently warm (Wood and Marsh 1996). This strategy could also be present in *L. capensis* but has yet to be confirmed. Observational or experimental work could further refine the ecological knowledge of this taxa and be beneficial for palaeoenviornmental intepretations of hydrological conditions. Like most phylactolaemates, living *L. capensis* colonies tolerate a water temperature range of 18–25 °C (Lacourt 1968), yet, dormant statoblasts can survive much wider extremes, which likely occur at this high elevation site.The relatively cool water at this high elevation, equatorial location suggests persistence at water temperatures below 18 °C. The inventory of tropical and African phylactolaemata fauna requires further investigation to understand distributions and the natural history of these taxa (Wood 2002).



Figures 5–8. *Lophopodella capensis* statoblasts and organic detritus, including charcoal at right, from the sieved sediment subsample from25–26 cm stratigraphic depth, dated to 220–230 yr BP (**5**). A well preserved statoblast observed at 41–42 cm, dated to 670–711 (**6**). Pleistocene-aged statoblast from 480–481 cm, dated to 15600–15700 (**7**). Same specimen as Fig 6 showing the split layers of the polar spine and recurved hooks (**8**).

Additional radiocarbon dates of the sediment stratigraphy could further constrain the presence data of this taxon. We suggest that presence data of bryozoan macroremains, including the resistant chitinous statoblasts and floatoblasts be examined in other sedimentological studies in East Africa (Francis 2001) as they remain an infrequently used indicator of aquatic palaeoenvironments and the potential of this proxy is not being realised. In addition these results contribute to our knowledge of African Phylactolaemata natural history. The results of such palaeodistributions can be submitted and archived in palaeoecological databases such as Neotoma (Goring et al. 2015). The new finding also suggests that Phylactolaemata should be considered more centrally in biodiversity surveys of macroinvertebrates of Kenyan wetlands. New studies of African phylactolaemata are necessary to understand biodiversity loss, local indicators of water quality fluctuations, changes to ecosystem function and as part of developing and incorporating nature-based solutions into local-level land management plans.

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